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Ecosystem services and disservices of ants in subsistence farming (Limpopo Province): an experimental approach in mango orchards.

By

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DECLARATION

I, Vongani Terrence Maphote, hereby declare that this MSc research project submitted by me to the University of Venda for the degree of Masters of Science in Zoology, is my original work and has not previously been submitted to this University or any other institution. I further declare that all the sources used in this work will be acknowledged.

Student

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ABSTRACT

Subsistence farming increases food security in households by improving human nutrition and cushioning against food price inflation. The mango is a particularly nutritious fruit cultivated and consumed in the Limpopo region, and insect communities may contribute by increasing its quality and productivity by means of pest control and pollination. Ants often dominate invertebrate assemblages in these orchards and the transformation of natural vegetation in and around agricultural production landscapes could lead to the reduction of ecosystem services for subsistence farming.

This study evaluates the ecosystem services and disservices provided by ants in largely transformed vs. mainly natural landscapes. Ten orchards, five in a natural landscape and five in a transformed landscape, were set out in a subtropical region of southern Africa. In each orchard ants were excluded from six trees and six acted as control. Ant abundance was monitored, flower visitors observed and yield quantified. Causal relationships were explored using Generalized Linear Fixed Effects Models and Structural Equation Models. Increased land transformation lead to a significant increase in ant abundance and richness, ant diversity had a significant negative impact on other flower visitor abundance and diversity. While other flower visitor diversity had a significant positive effect on yield, mango fruits had significantly more fungal contamination in trees where ants were excluded.

Ants therefore provided both services (pest control) and disservices (decreased flower visitor diversity) which were mediated by levels of transformation in the landscape. This has important implications for crop yield on small holder farms.

Keywords: Ants, ecosystem services, pollination, flower visitors, pests, *Mangifera indica*, yield, farms, Thohoyandou.

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CHAPTER 1: INTRODUCTION

Almost 50% of humans in sub-Saharan Africa are said to be malnourished, and many of these live in smallholder households (Steward et al., 2014). The extent of villages and commercial orchards in the Limpopo region of South Africa has increased considerably over the last few decades and in 2002 smallholder farmers numbered 273 000 (Statistics South Africa, 2002). These changes could affect ecosystem functioning related to crop yield in smallholder and commercial systems, underlining the importance of research into the response of pollination and biocontrol services. However, studies of ecosystem services such as pollination and biocontrol in small-scale farming (in Africa in general) has been neglected (Steward et al., 2014).

Anthropogenic activities have altered landscapes worldwide through agriculture and forest clearance (Fischer and Lindenmayer, 2006). This transformation has led to a concomitant decrease of heterogeneity in agricultural landscapes. Unfortunately, heterogeneity plays a major role in maintaining the viability of agricultural and ecological systems (Nelson et al., 2009) and humans depend on various services delivered by ecosystems. Amongst others, these services include soil productivity, water availability, pest control and animal-mediated pollination of crops. Anthropogenic activities often to decrease species diversity and change dominance within communities (Vandermeer, 2011). Moreover, anthropogenic disturbances favour/increase the abundance dominance of native or invasive ant species (Gibb and Hochuli, 2003).

Ecosystem service agents such as pest control or pollination are in decline through environment alteration (Vandermeer, 2011). Daily (1997) provided the definition of ecosystem services as "the conditions and processes through which natural ecosystems, and the species that make them up sustain and fulfill human life". The functioning of these ecosystem services and ecosystem disservices depends on the maintenance and management of agricultural ecosystems, and also on the diversity of the surrounding natural landscape (Tilman, 1999). Ecosystem services and disservices rely on a complex complement of direct and indirect interactions which link various functional groups such as pollinators, pathogens, predators and herbivores (Vandermeer et al., 2010).

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Ecosystem services include pollination, water purification, dung burial, food sources, natural control of plant pests and provision of habitat for insects in the agricultural habitat (Zhang et al., 2007). Agricultural intensification which results in the loss of natural habita can promote ecosystem disservices such as pest damage increase through removal of natural enemies, nutrient runoff and the use of pesticide has led to the development of genetic resistance of pest species triggering pest outbreaks and resurgence. (Zhang et al., 2007).

Ecosystem disservices can be associated with the reduction of yield, e.g. through predation (plant damage) by insect herbivores (Brown et al., 2006). There is increasing evidence that conserving wild pollinators in habitats next to an agriculture field increases the constancy of pollination, which results in higher yields (Klein et al., 2003). Most of the ecosystem services are provided by organisms that rely on habitat availability because such organisms need availability of resources at the landscape scale of foraging ranges (Kremen et al., 2007).

Agricultural landscape matrices that include natural habitats could provide a variety of resources for insects such as pollinators (Suzuki et al., 2009). The insect communities (flower visitors, ants, pests and biocontrol agents) providing these services (ecosystem services and ecosystem disservives) are influenced by local management and the surrounding landscape (Motzke, 2015). Therefore, it is important to determine how local management, especially of smallholder polyculture and conventional plantations, as well as the surrounding landscape such as village size and availability of natural habitats, affect insect communities and how this in turn affects service provisioning and functioning. The resulting knowledge is important if we are to develop and sustain management plans that will close yield gaps and support smallholder farmers (Motzke, 2015).

Services and disservices of ants

Ants are extremely abundant insects worldwide, representing 20–40% of all arthropod biomass (Davidson et al., 2003). They are likely to have a major impact on the structure of plant–insect food webs at both ecological and evolutionary scales (Heil and McKey, 2003). Ants are, for instance, considered to be the keystone group of invertebrate predators in tropical forests (Olson, 1992). Many ant species have mutualisms with plants or insect herbivores (Davidson et al.,

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2003). This mutualism may supply the major resources needed to maintain the remarkably high biomass of ants in tree canopies (Hunt, 2003).

Ants increase the production of fruit set and seed dispersal while decreasing the damage caused by folivores in Africa (Table 1) (Carvalheiro et al., 2010; Sung et al., (2006)). It is said that ants contribute more than 40% to the fruit set of mangoes (Carvalheiro et al., 2012), and in tropical regions ants are known to control a variety of natural pest species in mango orchards (Lauer, 2014; Henri et al., 2015). As a result, ants do not only maximize the production of mangoes through pollination services, they also increase the quality by controlling pests (Henri et al., 2015).

Competition between ants and other flower visitors for floral rewards can alter the visitation of other flower visitors' behavior during pollination (Ohashi et al., 2008). Ants are said to be the most common flower visitors attracted to nectar (Lach, 2005), where they tend to protect such nectar reward against any other flower visitors (Altshuler, 1999). Ants can thus alter the attraction of flowers by preventing other flower visitors from foraging at the flowers for nectar (Cembrowski et al., 2014). An increase in ant abundance led to the increased harassment of bees, reducing the accessibility of nectar and their length of visits (Cembrowski et al., 2014).

Few mango growers regard ants as a pest (disservices), although they can cause black spots on the mango fruit through the production of formic acid (Peng and Christian, 2005; Peng, 1995). Peng and Christian (2005) observed mutualistic relationships between ants and mealybugs (pests) found in the flower stem as well as between ants and flat/fluted scales (pests) found on the leaves, resulting in mango fruit damage of up to 30%.

Pollination

Pollination contributes to 35% of the production of the commercially most important crop plants worldwide (Klein et al., 2007) and the global number and proportional estimate of animal pollinated angiosperms was at 308 006, which is 87.5% of the estimated species-level diversity of flowering plants (Ollerton et al., 2011). The majority of crops such as sugar apple, turnip rape, canola, oilseed rape, watermelon, grapefruit, coffee, longan fruit, sunflower, tomato and

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macadamia nut thus depend on pollinators (Klein et al., 2007) and the importance of this pollination service in 2005 has been valued at €153 billion worldwide (Gallai et al., 2009).

The frequency of flower-visitors and diversity of pollinators in crop fields are greatly affected by the separation between crop fields and natural habitat, resulting from fragmentation (Garibaldi et al., 2011), although it can be beneficial to fragmented patches of natural or semi-natural habitat for pollination, as these may have a high number of pollinators conserved within their isolated areas (Kremen et al., 2002). When agricultural landscapes are properly managed, a suitable habitat can be supplied for many insect species (Tscharntke et al., 2005). Similarly, wildlife-friendly farming may sustain pollinator populations and pollination services in heterogeneous agricultural landscapes (Tscharntke et al., 2005).

However, pollinators are threatened by different anthropogenic drivers such as habitat loss and pesticide use. Agricultural intensification can lead to a loss of flower resources and nesting sites, resulting in the decline of pollinators. The resulting pollinator limitation can threaten crop production (Tscharntke et al., 2005).

That decreases in pollinator populations are often linked to human activity has been well documented (Potts et al., 2010; Ghazoul, 2005). Furthermore, there is considerable concern over the decline in pollinators in Britain and Netherlands (Biesmeijer et al., 2006). Most studies suggest that bees (wild and managed bees) are the major pollinator taxon in most ecosystems for crop yield (Axelrod, 1960; Rader et al., 2016), and their sensitivity to the loss of natural and semi-natural habitats is well recorded (Kremen and Chaplin-Kramer 2007).

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Table 1: Percentage of flower visitors to different cultivars of mango on different continents: Col.= Coleoptera, Lep. = Lepidoptera. Hym. = Hymenoptera and Hem= Hemiptera.

Varieties	Region	Hymenoptera (Apidae)	Diptera	Hymenoptera (Formicidae)	Coleoptera	Lepidop-tera	Others	Study paper
Irwin, Jinhwung No. 1, Tainong No. 1 and Tsai-Swain	Taiwan	10	42	<1	5	2	Hemiptera 12	Sung et al., (2006)
-	Costa Rica	4 *[1]	52	-	12	33	-	Jiron and Hedström (1985)
Kent	South Africa	16*[2]	26	43	12	<1	3	Carvalheiro et al., (2010)
	India	52	45	0	<1	<1	3	
	Bangla-desh	26*[1]	52	0	0	0	16	Mohan et al., (2013)

*1: All Hymenoptera included

*2: 58% Honey bees, including wild and managed hives

Mangifera indica

Mango (*Mangifera indica* L., Anacardiaceae) is native to India, Malaysia, Myanmar and Bangladesh and is a vital fruit crop in tropical and subtropical lowland regions (Griesbach, 2003). The mango plantation needs tropical climate at low altitudes and winter dry seasons for flowering and fruit set (Watson and Dallwitz, 1999).

Mango is among the most widely cultivated and consumed fruit crop in the Limpopo Province (pers. obs.). The rapid increase of subsistence production in the Limpopo region has improved the food security of poor households by increasing food supply and reducing dependence on obtaining food in a high inflation environment (Baiphethi and Jacobs, 2009). Carvalheiro et al. (2010) found that the final production of two mango cultivars was significantly affected by isolation from natural habitat, the result on mango production being associated with the decline in flying visitors.

The flowers of mangoes are unspecialized, allowing pollination by a diversity of insects (Heard, 1999). This diversity of insects pollinators play a positive role by increasing the fruit set of mango flowers, in the sense that complementarity between varieties of pollinators can lead to

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optimal utilization of all flowers in a tree and maximize the fruit set in each and every inflorescence (Free and Williams, 1976; Carvalheiro et al., 2010). It is therefore important to know that flower visitors have a high sensitivity to fragmentation or isolation from natural habitats (Siqueira et al., 2008).

Pests and Diseases

Heterogeneity in natural vegetation promotes a local density of natural enemies, and thus pest control, through the supply of shade and shelter (Heimpel and Jervis, 2005). A variety of landscapes may benefit biocontrol agents through the supply of food sources such as pollen and nectar from plants and proteins and lipids from insects. (Macfadyen et al., 2011; Heimpel and Jervis, 2005). Increasing isolation between agricultural fields and natural vegetation will thus result in a decline in the abundance and diversity of natural enemies, which could lead to the reduction of pest management and decrease in crop productivity (Henri et al., 2015).

There are four major orders that include important pest species of mangoes:

Hemiptera: e.g. *Aulacaspis tubercularis* is a scale insect that affects the leaf of a tree and turns it into pale green or yellow, then later the leaf dies, reducing photosynthesis (Bally, 2006).

Lepidoptera: e.g. *Penicillaria jocosatrix* and *Chlumetia euthysticha* are often a serious pest during hot, wet, summer seasons, where the larvae of these species penetrate and destroy the developing flushes (Bally, 2006) (Table 2).

Diptera: e.g. *Procontarinia matteiana* is a leaf-gall-forming fly, which affects the leaf of a mango by reducing the photosynthesis of a tree (Henri et al., 2015). *Ceratitis* spp., *Dacus* spp. and *Strumenta* spp. are fruit flies, where the adults lay eggs before, during and after the harvest period and larvae eat throughout the flesh, causing rot (Henri et al., 2015).

Coleoptera: e.g. *Sternochetus mangiferae* penetrates seeds in the early developmental stage of the fruit with less harm to the fruit, destroying the cotyledons of the seed and reducing germination success (Bally, 2006).

These pest species (Table 2) are major barriers to export (Bally, 2006).

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Diseases such as powdery mildew (cause defoliation) and anthracnose (cause small black spots) are common and widespread fungus diseases of mango and are serious diseases which affect production in areas where conditions are favorable (Yahia, 2011; Griesbach, 2003). Fungus attack inflorescences, fruits, leaves, twigs, buds, flowers and young fruits of a mango cultivar (Griesbach, 2003).

Table 2: Mango pests and their parasitoids/antagonists in South Africa. From Peña et al. 2002; Rehman *et al.* 2013; CABI 2014, altered by Lauer (2014).

Common name of mango pests	**Latin name(s)**	**Part of the plant**	**Their parasitoids/ antagonists**
Seed weevils	*Sternochetus mangiferae*	Fruits, seeds	*Beauveria bassiana (fungus)*
Fruit flies	*Ceratitis capitata, C. cosyra , C. rosa*	Fruit	*Coptera silvestrii*
Coconut bug	*Pseudotheraptus wayi*	Young green, fruits terminal, leaf petioles	*Oecophylla longinoda (weaver ant)*
Tip wilter	*Anoplocnemis curvipes*	Leaf veins flower stalks of young trees	*Hermyra sp., Pheidole megacephala* (ant)
Thrips	*Scirtothrips aurantii Selenothrips rubrocinctus*	Small green fruit Leafs, near to the midrib	Robber mites: *Amblyseius tutsi, Euseius addoensis, E. citri, E. orygmus*
Gall midges	*Procontarinia matteiana*	Leafs	*Closteroceru s pulcherrimus*
Mango scale	*Aulacaspis tubercularis*	Fruit, leafs discolored	Parasitic wasp: *Encarsia citrina,* Lady bugs: *Rhyzobius lophantae, Chilocorus nigritus, Thrips: Aleurodothrips fasciapennis*
Soft scales	*Milviscutulus mangiferae*	Diverse whole tree	*Cocophagus pulvinariae, Marietta javensis*

Research problem

The Limpopo region has seen a rapid increase in it human population and associated developmental impacts (Statistics South Africa, 2002). The most pervasive of these is the conversion of natural vegetation into crops and rural/urban residences (Steward et al., 2014). Studies have shown the importance of native vegetation for the provisioning of ecosystem services in agricultural land, but these studies have largely focused on commercial agriculture

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with very little attention given to subsistence farming, the dominant land use option for rural people in the region (Steward et al., 2014).

As a dominant component of insect assemblages, ants play a central role in the provisioning of ecosystem services and are important pollinators and pest control agents in mango orchards (Henri et al., 2015). However, there are few experimental evidence exists for these observations. The effect of ants on pollinator abundance and diversity, mango fruit set, and yield as well as the interaction with land use change require better understanding if we are to manage food security in a changing environment.

Only 12% of pollination and biological control studies include smallholder farmers (Steward et al., 2014) because the majority of research studies of the agriculture in Africa are done at larger scale in the form of commercial farming. A better understanding of the role of ants and landscape characteristics on an important crop such as mango should identify design principles that could guide optimized production in landscapes that are predicted to experience considerable change.

Aim and objective

To quantify the impact of ants and land use (level of landscape transformation) on pollinator diversity and abundance, and on yields of mangoes, on smallholdings.

Hypotheses

Ants have a negative effect on the abundance and richness of pollinators, and a positive effect on yield in mango orchards

Ants act as natural enemies of pests in mango orchards.

Surrounding land use, in terms of cultivation/human settlement vs natural, has a negative effect on the abundance and diversity of pollinators, and also on yield in mango orchards.

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CHAPTER 2: METHODOLOGY

Study background, site and design

Thohoyandou is situated in the Limpopo Province, 70 km east of Louis Trichardt in South Africa, and receives around 95% of the average rainfall of the region, which is about 800 mm (of 95% of average rainfall) (M'marete, 2003). The wet season is between October and March (M'marete, 2003). The Thohoyandou region experiences temperatures which vary daily between 25˚C and 40˚C in summer and between 22˚C and 26˚C in winter (Mzezewa et al., 2010). The soil type of the area consists mainly of red and leptosol (poorly drained with an apedal structure), where the clay content is mostly high (60 %) and soil reaction is acidic (pH = 5.0) (Mzezewa and Gwata, 2012). People on smallholdings depend on agriculture, planting fruits such as mango, banana, avocado and orange for nutrition and also for generating income.

The study sites were located in the farming region of Thohoyandou, where ten mango orchards were selected that were between 1 km and 30 km apart in semi-natural and natural areas (Figure 1 and Appendix 1). To assess the effects of the surrounding land-use on biodiversity and ecosystem services at the local farm scale, the ten sites differed with respect to the proportion of surrounding natural (untransformed) habitat, in order to quantify the level of transformation: five orchards whose surrounding matrix were in mostly untransformed (≥ 70% natural habitat), the other five orchards were situated in landscapes that were largely transformed (≤ 30% natural habitat) (Figure 2). None of the farms used pesticides or herbicides in the management of crops, and all used one mango cultivar, Sabre.

Sabre originated in South Africa in 1928 and is one of the most popular cultivars. The tree is medium in height and the harvest season lasts from December until February. The tip (apex) of the fruit is round and curved into a projecting beak. It has a smooth skin, which is green-yellow in color (Davis, 1928). The flesh is orange in color. Sabre does well at higher elevations, produces good quality fruit, is resistant to fungal diseases that affect a variety of plants in warm or humid areas and is widely preferred as a rootstock producer (Davis, 1928).

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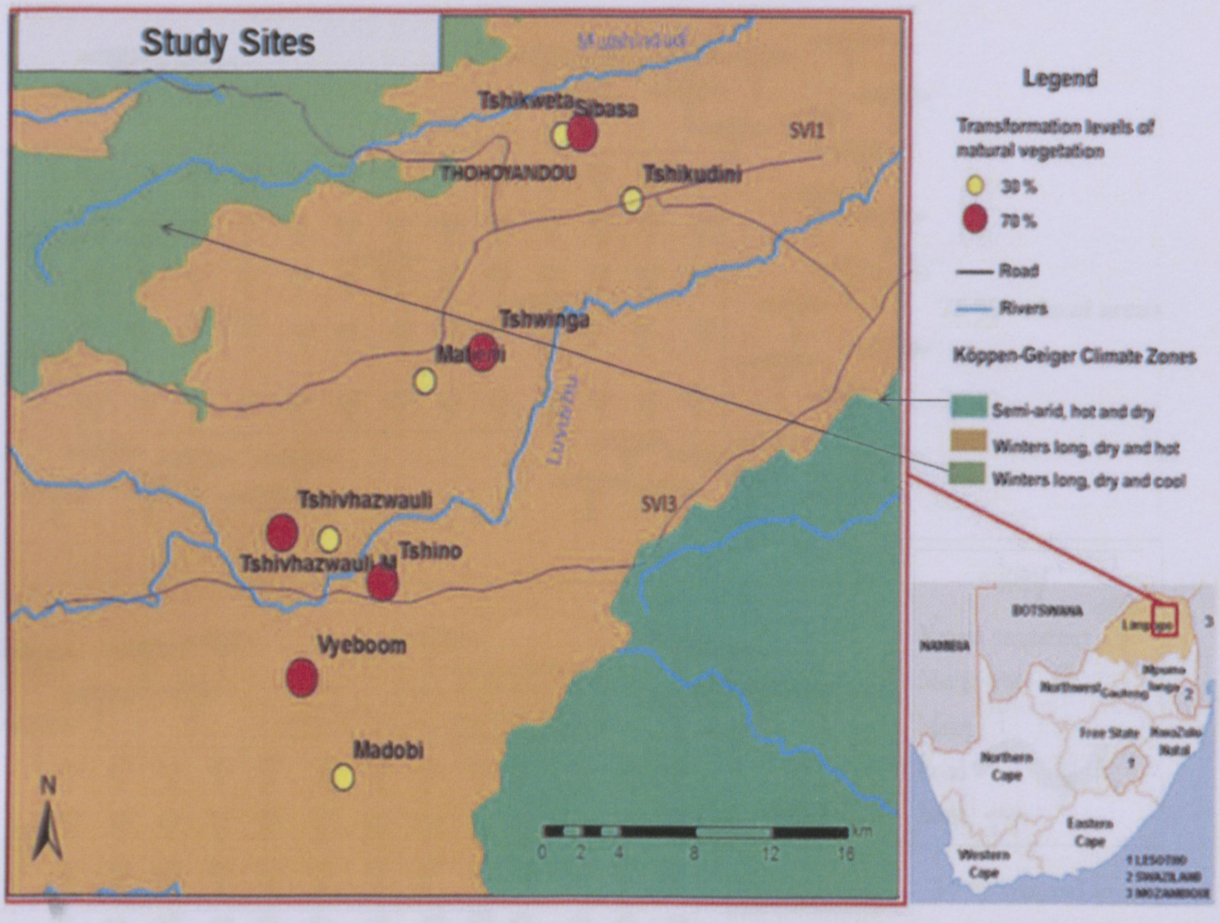


Figure 1: Map of the ten study sites located in the surroundings of Thohoyandou, Limpopo Province, South Africa. Image source: ArcGIS version 10.2.2.

A total of 12–14 trees were randomly selected within each orchard to quantify the effect of ground cover and their size (width and height) did not differ much within/between the orchard. To assess the importance of ants for pollinator visitation and crop yield, treatments were randomly allocated to these trees. Half of the selected trees per orchard acted as controls while the other half were given exclusion treatments. Ants were excluded, or their abundance at least significantly reduced, by using duct tape, cotton and TANGLEFOOT® around the main stem of the tree (Figure 3). The controls received no such treatment. This was done and its effectiveness evaluated four months before the mango flowering season started in July.

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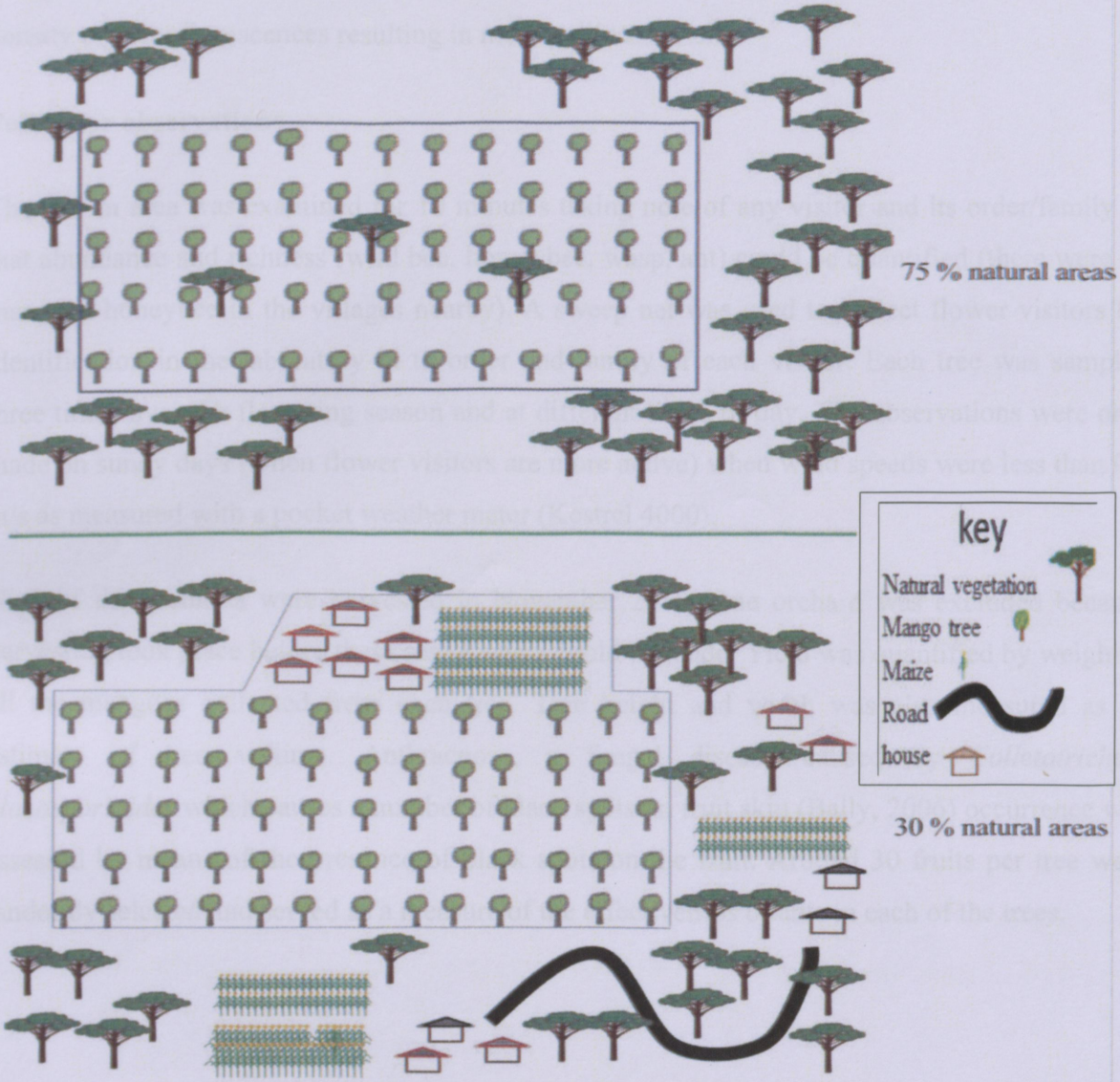


Figure 2: The study site design, showing variations of mango orchards and their surrounding natural vegetation.

Pollination studies

Flower abundance: Mango flowers are hyperabundant and five inflorescences were selected at random within a created 2×2 m section in each and every sampling tree in the selected orchard and the number of flowers counted. This was used to provide two estimates of inflorescences: one, by scaling up, to give the total abundance of inflorescence of each tree as a whole, and one

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of the 2x2 m area that was observed. This was done to control for the possible effect of higher density of the inflorescences resulting in more pollinator visits.

Pollinator observations

The 2x2 m area was examined for 10 minutes taking note of any visitor and its order/family so that abundance and richness (wild bee, honey bee, wasp, ant) could be quantified (there were no managed honeybee in the villages nearby). A sweep net was used to collect flower visitors for identification in the laboratory in to order and family of each visitor. Each tree was sampled three times over the flowering season and at different times of day. The observations were only made on sunny days (when flower visitors are more active) when wind speeds were less than 0.1 m/s as measured with a pocket weather meter (Kestrel 4000).

Nine of the orchards were harvested in November 2015. One orchard was excluded because harvesting took place before these assessments could be made. Yield was quantified by weighing all the mangoes collected from each tree. Tree height and width was also measured as an estimate of tree volume. Anthracnose, a fungal disease caused by *Colletotrichum gloeosporioides* which causes a number of black spots on fruit skin (Bally, 2006) occurrence was assessed by means of the presence of black spots on the fruit. Around 30 fruits per tree were randomly selected and served as a measure of the effectiveness of ants in each of the trees.

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Figure 3: Procedure for setting up ant exclusions: A) Duct tape was wrapped around the main stem of the tree, B) this was then covered with a roof sealing membrane, C) which were then covered with duct tape again, D) and finally TANGLEFOOT® (glue) was smeared over the duct tape.

Statistical analysis

Generalized linear mixed-effects models (GLMMs) with a log-link function and Poisson error distribution were used to quantify the effectiveness of ant exclusions after the bush beating method had been used. The impact of ants and the surrounding vegetation on the activities of flower visitors were assessed by modelling their abundance using GLMMs with a log-link function and a quasipoisson error distribution (data were overspread) (time period as fixed variable and orchards as random variables) across three time categories: morning 08h00–11h00, midday 11h00–13h00 and afternoon 13h00–15h00. Generalized linear mixed models are a powerful class of statistical model that combine the characteristics of generalized linear models

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and mixed models, i.e. models which include both fixed and random predictor variables (Kachman, 2000). They handle a wide range of response distributions and a wide range of states where observations have been taken in groups rather than completely independently (Işık, 2011).

Path Analysis was used to study the causal relationships between two or more variables (Figure 4). It is based upon a linear equation system and it was first developed by Sewall Wright in the early twentieth century (Wright, 1920). It is a generalization of many regressions that allows the estimation of the strength and sign of directional relationships for complicated arrangements with various dependent variables (Li, 1975).

Structural Equation Modeling is a comprehensive statistical approach testing hypotheses about relations among observed and latent variables (Hoyle, 1995). It is a methodology used for representing, estimating, and testing a theoretical network of (mostly) linear relations between variables (Rigdon, 1998). It also tests hypothesized patterns of directional and non-directional relationships among a set of observed (measured) and unobserved (latent) variables (MacCallum and Austin, 2000). Structural Equation Modeling (SEM), which is the combination of linear mixed effects models (lmer), with the following package: lme4 and piecewiseSEM was used to analyze the path relationship between the response and the predictor variable.

Linear mixed-effects models were used to explore the effect of ant abundance and richness on the average amount of black spot (pest) per tree in each orchard. Furthermore, linear mixed-effects models were used for modeling the relationship between fixed factor (ant abundance and richness) and random factor (Orchard and tree individual) (e.g. Işık, 2011). All statistical tests were done in R vision 3.2.4 (R Core Team, 2016).

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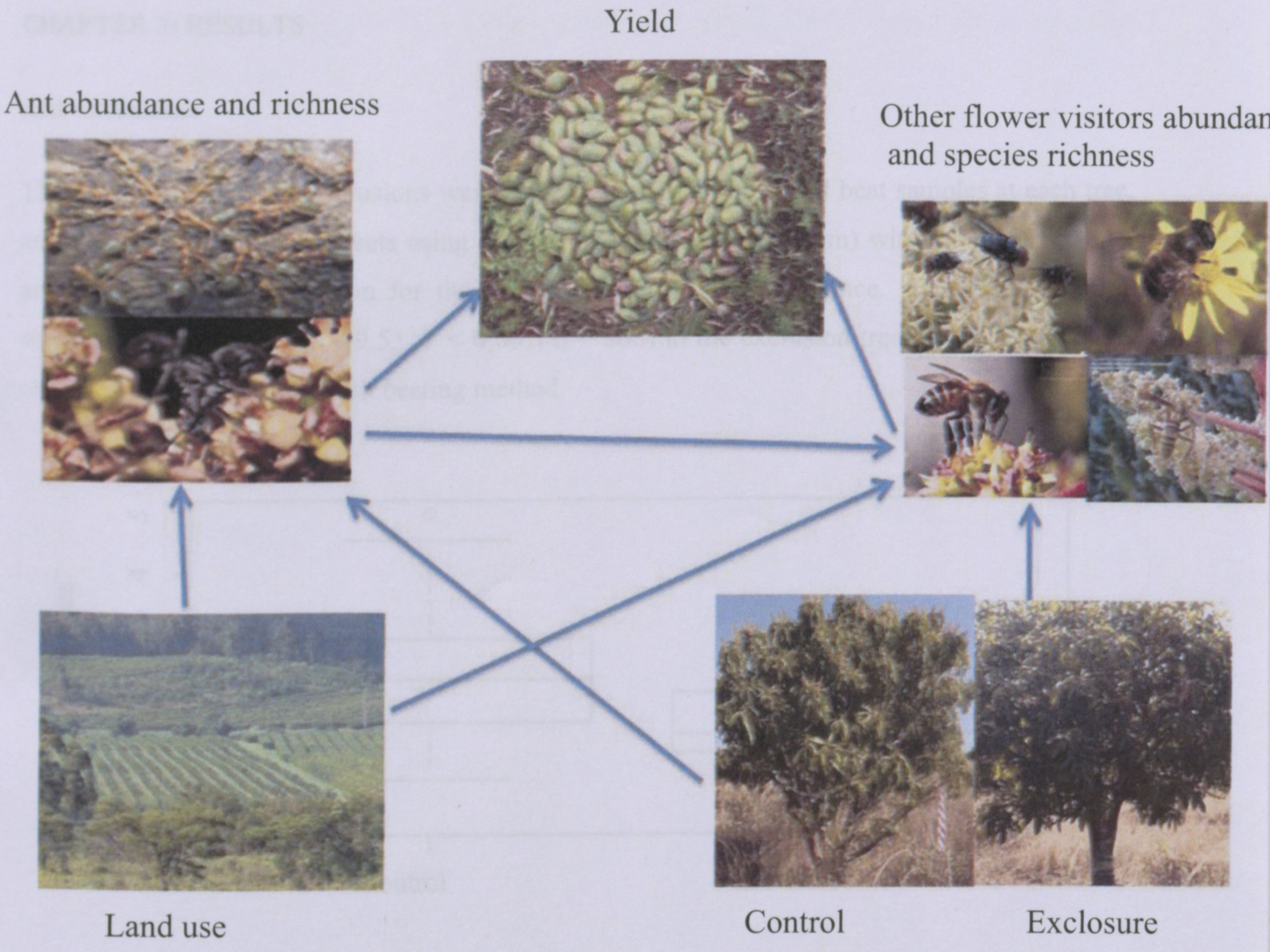


Figure 4: Hypothesized path diagram of the causal relationships between land use, other flower visitors (abundance and diversity), ants (abundance and diversity) and mango yield.

The path diagram as illustrated in Figure 4 shows the nature and direction of the hypothesized relationships. In addition, the strength of those relationships and the path coefficients (p) need to be understood. A path coefficient is the standardized slope of the regression of the dependent variable on the independent variable in the context of the other independent variables.

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CHAPTER 3: RESULTS

Ant exclusion

The effectiveness of the exclusions was assessed by taking 30-second beat samples at each tree, and tested for significant effects using a generalized linear model (glm) with a loglink function and Quasipoisson distribution for the response variable, ant abundance. Ant abundance was significantly reduced ($z = -19.53$, $P < 0{,}001$, $n = 260$) in the exclusion treatment (Figure 5), as observed by means of the bush beating method.

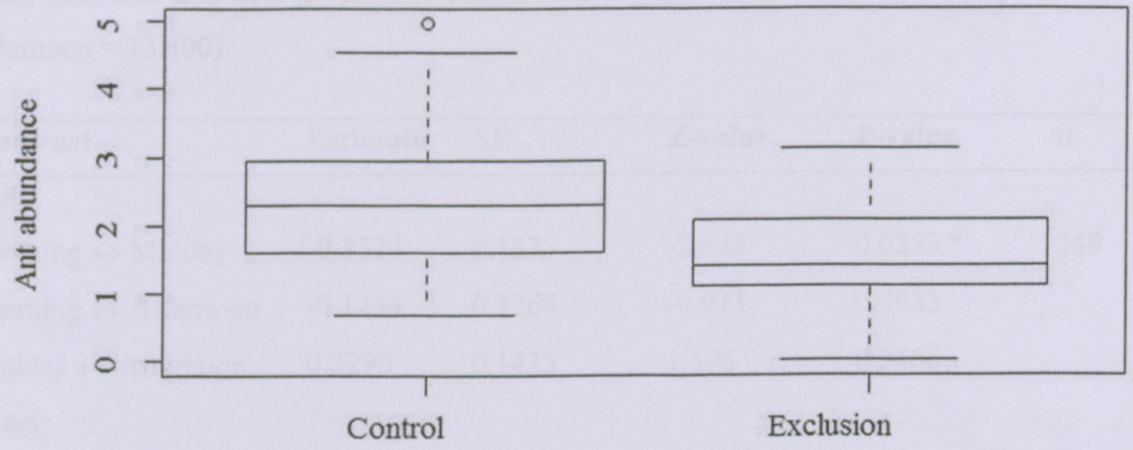


Figure 5: Box-and-whisker plot showing the abundance of ants for the period of three months (March, April and May 2015) from bush beating sampling.

Pollination

A total of six orders and 33 insect families were observed during the mango flowering season of August through September 2015 (Appendix D). Hymenoptera were the most abundant flower visitors at 70.75%, followed by Diptera at 27.89 % (Appendix D). The three most common Hymenoptera flower visitors observed in the mango orchards were ants (41% Formicidae observed,) comprised of 5 genera (*Camponotus*, *Crematogaster*, *Polyrhachis*, *Lepisiota* and *Tetraponera*), honey bees with one species (*Apis mellifera, 11%*) and one species of Pteromalid

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wasps (9%). The flower visitor of the family Calliphoridae (flies, 48% observed within the order Diptera) contributed the most during pollination in the mango orchards.

Analysis of the pollinator abundance suggests that there was temporal partitioning of flower visitation times for the three dominant flower visitor groups which were Formicidae (ants), Diptera (flies) and *Apis mellifera* (honeybees). Bees were more active during midday (11h00–13h00) and Diptera in the morning (08h00–11h00) and afternoon (13h00–15h00) (Table 3; Figure 6). Ants were found to be active throughout of the day (Figure 6).

Table 3: Results of Generalized Linear Model with quasipoisson distribution of abundance of flies, bees and ants at a given time period in a day (morning = 08H00, midday = 11H00 and afternoon = 13H00).

Contrast	Estimate	SE	Z-value	P-value	n
Flies					
Morning ↔ Midday	-0.3524	0.1333	-2.643	0.0223 *	349
Morning ↔ Afternoon	-0.1234	0.1268	-0.973	0.5933	
Midday ↔ Afternoon	0.2290	0.1435	1.596	0.2466	
Bees					
Morning ↔ Midday	0.2520	0.2720	0.926	0.621	349
Morning ↔ Afternoon	-0.5112	0.3458	-1.478	0.299	
Midday ↔ Afternoon	-0.7631	0.3411	-2.237	0.064 ·	
Ants					
Morning ↔ Midday	-0.6492	0.4893	-1.327	0.378	349
Morning ↔ Afternoon	-0.4419	0.4662	-0.948	0.608	
Midday ↔ Afternoon	0.2073	0.5565	0.373	0.926	

Levels of significance other than (p): · = 0.1, * = 0.05, ** = 0.010, *** = 0.001

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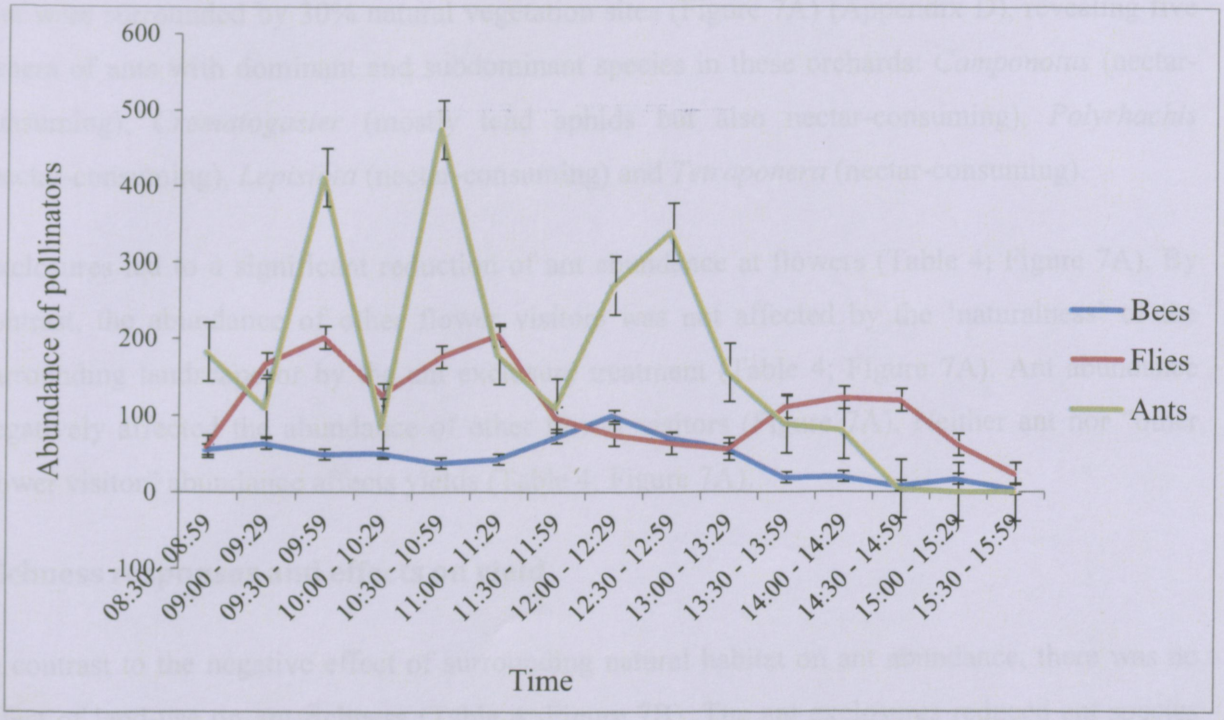


Figure 6: Dynamics of the total of pollinator abundance (error bars with standard error) throughout the day summed up over all study sites.

Yield

The total mango yield of trees without exclusions was higher than that of trees where ants were excluded (18.03 kg vs. 13.73 kg, the average of all trees with a standard deviation of 2.26 and 1.67 respectively) (Appendix C). An average of 76.05 kg (standard deviation of 50.45) was recorded in orchards that were surrounded by 30% of natural vegetation and an average of 69.59 kg (standard deviation of 35.87) was recorded within the orchards that were surrounded by 70% of natural vegetation (Appendix B).

Structural Equation Modeling (SEM)

Flower visitor abundance

The orchards which were surrounded by more than 70% natural vegetation had fewer flower visiting ants compared to orchards whose surrounding vegetation were more transformed (30% surrounding natural vegetation) (Table 4; Figure 7A). Furthermore, ant abundance was negatively related to surrounding natural vegetation in that ant abundance was higher in orchards

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that were surrounded by 30% natural vegetation sites (Figure 7A) (Appendix D), revealing five genera of ants with dominant and subdominant species in these orchards: *Camponotus* (nectar-consuming), *Crematogaster* (mostly tend aphids but also nectar-consuming), *Polyrhachis* (nectar-consuming), *Lepisiota* (nectar-consuming) and *Tetraponera* (nectar-consuming).

Exclosures led to a significant reduction of ant abundance at flowers (Table 4; Figure 7A). By contrast, the abundance of other flower visitors was not affected by the 'naturalness' of the surrounding landscape or by the ant exclosure treatment (Table 4; Figure 7A). Ant abundance negatively affected the abundance of other flower visitors (Figure 7A). Neither ant nor "other flower visitor" abundance affects yields (Table 4; Figure 7A).

Richness responses and effects on yield

In contrast to the negative effect of surrounding natural habitat on ant abundance, there was no effect of land-use on ant richness (Table 4; Figure 7B). The ant exclosures reduced ant species richness while the richness of other flower visitors was unaffected (Table 4; Figure 7B). Ant richness did not affect mango fruit yield. However, yields responded positively to the richness of other flower visitors (Table 4; Figure 7B). Ant richness therefore had an indirect negative effect on mango yield by having a negative impact on the abundance of other flower visitors (Table 4; Figure 7B).

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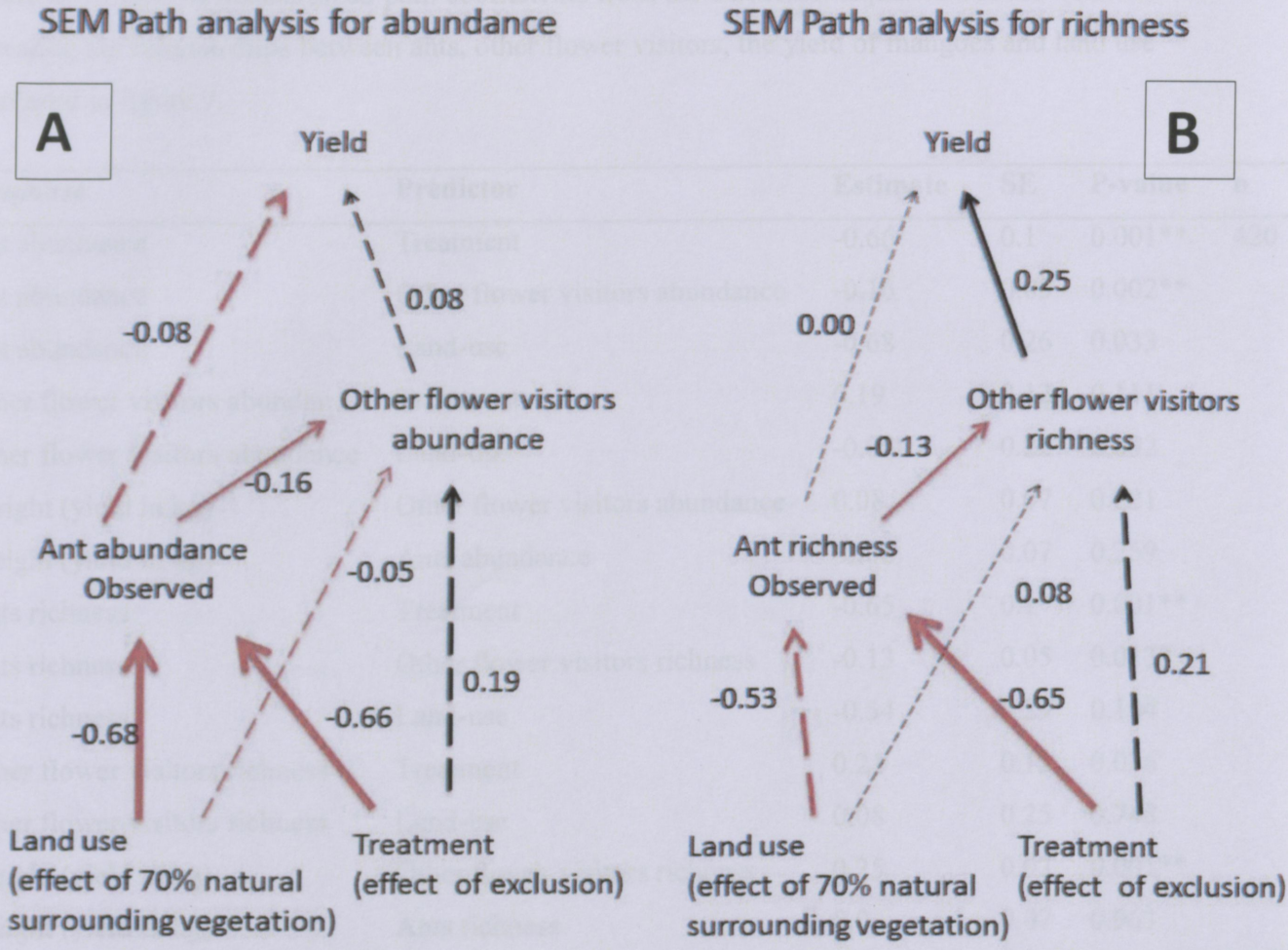


Figure 7: Results from Structural Equation Modeling (Table 4) on (A) abundance effects of ants and other flower visitors or (B) richness effects of ants and other flower visitors on Mango yield. These models also incorporate the effects of surrounding land-use (30% vs 70% natural vegetation remaining) and of the ant exclosures (control vs. excluded). Dashed arrows indicate insignificant effects ($P>0.05$), while solid arrows indicate a significant difference ($P<0.05$). Red and black represent negative and positive effects respectively.

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Table 4: Results of standardized path coefficients from the Structural Equation Models (SEMs) revealing the relationships between ants, other flower visitors, the yield of mangoes and land use displayed in figure 7.

Response	Predictor	Estimate	SE	P-value	n
Ant abundance	Treatment	-0.66	0.1	0.001**	420
Ant abundance	Other flower visitors abundance	-0.16	0.05	0.002**	
Ant abundance	Land-use	-0.68	0.26	0.033	
Other flower visitors abundan	Treatment	0.19	0.12	0.111	
Other flower visitors abundance	Land-use	-0.05	0.22	0.832	
Weight (yield in kg)	Other flower visitors abundance	0.08	0.07	0.221	
Weight (yield in kg)	Ants abundance	-0.08	0.07	0.259	
Ants richness	Treatment	-0.65	0.1	0.001**	
Ants richness	Other flower visitors richness	-0.13	0.05	0.013*	
Ants richness	Land-use	-0.54	0.29	0.104	
Other flower visitors richness	Treatment	0.21	0.12	0.076	
Other flower visitors richness	Land-use	0.08	0.25	0.748	
Weight (yield in kg)	Other flower visitors richness	0.25	0.07	0.001**	
Weight (yield in kg)	Ants richness	0.0	0.07	0.963	

Levels of significance (p): ' = 0.1, * = 0.05, ** = 0.010, *** = 0.001

Pests

The fungal occurrence was significantly higher in exclosure treatments compared to that in control trees (Table 5; Figure 8).

Table 5: Results of Linear Mixed-Effects Models quantifying the effect of ant exclusion on fungal disease (pest).

Contrast	Estimate	SE	Z-value	P-value	n
Treatment (Control ↔ Exclusion)	0.34	0.09	3.78	0.0001***	420

Levels of significance (p): ' = 0.1, * = 0.05, ** = 0.010, *** = 0.001

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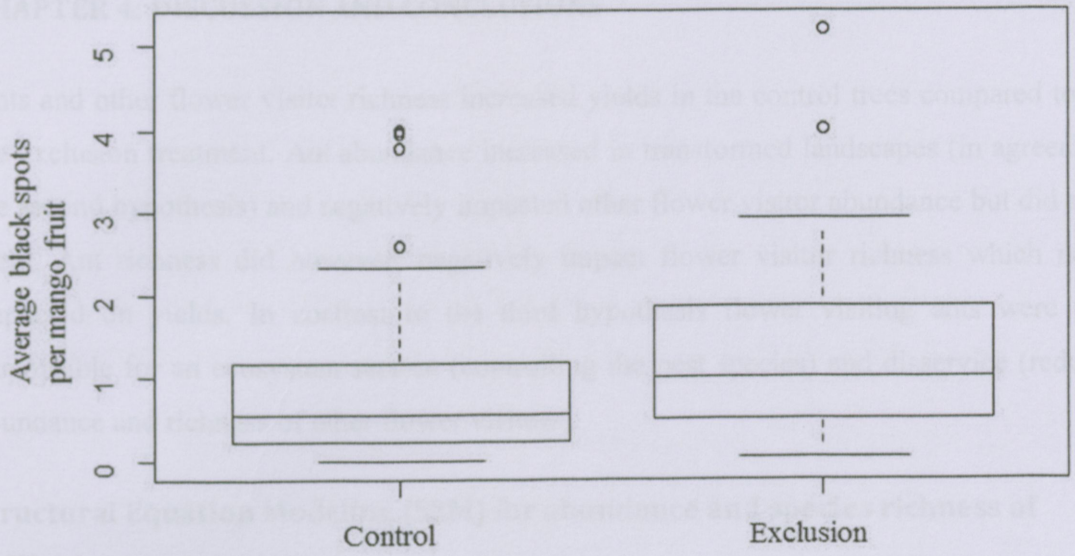


Figure 8 Pest infestation per mango fruit (number of black spots on the fruit skin) between control trees and trees with ant exclosure.

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CHAPTER 4: DISCUSSION AND CONCLUSIONS

Ants and other flower visitor richness increased yields in the control trees compared to those in the exclusion treatment. Ant abundance increased in transformed landscapes (in agreement with the second hypothesis) and negatively impacted other flower visitor abundance but did not affect yield. Ant richness did however, negatively impact flower visitor richness which negatively impacted on yields. In contrast to the third hypothesis flower visiting ants were therefore responsible for an ecosystem service (controlling the pest species) and disservice (reducing the abundance and richness of other flower visitors).

Structural Equation Modeling (SEM) for abundance and species richness of pollinators

Carvalheiro et al., (2010) found that species richness and abundance of flying pollinators decreased with distance from natural habitat, whereas ants were not affected. Land-use effects in this study were weak for other flower visitor richness and abundance. This suggests that ant abundance is either unaffected or increases in transformed landscapes.

Land use increases the abundance and diversity of flower visitors e.g. ants) in orchards surrounded by 30% natural areas compared to orchards surrounded by 70% natural areas (Appendix D). Although more flower visitors such as ants were increased in orchards surrounded by $\leq$ 30% natural habitat (Appendix D), the healthy diversity and abundance of pollinators depend on the variety of natural resources (Rundlöf and Smith, 2006), and such diversity and abundance of pollinators play important roles in maintaining pollination and yield (Carvalheiro et al., 2010; Kremen et al., 2002).

The presence of ants (abundance and species richness) is important for agricultural productivity and plays a major role by driving indirect and direct interactions such as pollination, pests and yields in the ecosystem (Wielgoss et al., 2014). Increases in ant abundance can alter the attractiveness of flowers by disturbing other flower visitors such as bumblebees during the search for nectar (Cembrowski et al., 2014). More than this, ant abundance and richness can reduce the accessibility of nectar to other flying pollinators (bees) by biting and harassing any visitors on the flower (Cembrowski et al., 2014).

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Pollination

High diversity and an abundance of flower visitors were observed on mango flowers during the peak of the pollination season (August to September). Ants were have been identified as effective pollinators some of mango cultivars (Carvalheiro et al., 2008) improving early fruit set. The abundance of ants on mango flowers throughout the day, though, led to a decrease in other flying visitors such as flies and bees (other flower visitors). As a result it seems that bees and flies had adapted a temporal partition of time of the day on the flowers (e.g. Stone et al., 1999).

Most of the flowering of plants is said to take place during the course of the day, creating temporal partitioning (Stone et al., 1996). Flower visitation by insects is associated with the number of flowers available on the tree (Stone et al., 1999). Furthermore, flower visitors frequently utilize plant species differently according to time of the day during the pollination season (Blüthgen and Klein, 2011; Willmer and Corbet, 1981). Flies and honeybees spend their time differently so as to maximize foraging strategy affected by competition and fluctuation of temperature. Ant species in general withstand temperature and competition as witnessed by the fact that they dominate flower visitation throughout the day.

Simiar to Stone et al., (1999) we found that some of the species (e.g. bees) of hymenoptera had indeed temporally structured their daily time while searching for food. This suggests that species of bees and flies have adapted to search for food within a specific time of a day so as to minimize competition with some of the flower visitors such as ants, creating temporal partitioning.

Yield

The rehabilitation of transformed areas in farmland is expensive (Ghazoul, 2007), but based on the results obtained in the course of this study, the amount of surrounding natural vegetation had no effect on flying flower visitor abundance or diversity. It did however affect ant diversity and abundance. Less ant diversity and abundance was observed in more natural surroundings and, as a result, a slight increase in mango production was observed in orchards which were surrounded by simple landscapes ($\leq$ 30% natural habitat) compared to complex landscapes ($\geq$ 70% natural habitat) (Appendix B). Klein et al., (2003) indicated that there has been increasing evidence that

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conserving wild pollinators in habitats adjacent to agriculture filed improves the stability of pollination, leading to increased yields and income.

In a study of coffee trees, species richness, compared to abundance, of solitary bees led to the increase of fruit set, maximizing the yield (Klein et al., 2003). Hoehn et al., (2008) also showed that species richness of bees significantly increases the seed set of pumpkins. On the other hand, in this study, species richness of ants did not affect or drive mango yield directly, but the richness of other flower visitors had a direct positive effect on the yield. The species richness of pollinators is more important than abundance, which indicates that the complementarity of flower visitors drives mango yield, and not the dominance of a single abundant species. Complementarity between pollinators and pollen dispersal maintains these ecosystem services (Kremen et al., 2002).

The flowers of mango trees are unspecialized, meaning that they allow a variety of flower visitors such as bees, wasps, flies and ants for pollination at different heights of the tree (Heard, 1999). These flower visitors have different body lengths, maximizing pollination and so maintaining mango yield. Hoehn et al., (2008) indicated that bee species differ in their flower visitation times and also above ground preferences associated with their body size.

In a cacao plantation an ant-exclusion treatment led to a decrease in yield during harvest, from 600 kg to 300 kg of (Gras et al., 2016; Wielgoss et al., 2014). Just as in this study, where control trees were found to have a high yield of mangoes (1045.5 kg) compared to trees where ants were reduced, for which mango production was low (808 kg).

Pests

Gras et al., (2016) found that the presence of ants in both control and exclusion treatments on cacao trees did not have an impact on fungal growth. Infestation by pests also increased when ants were reduced or excluded in treatments, leading to negative effects on fruit weight and yield of cacao (Wielgoss et al., 2014). In the current study, the treatments where ants were highly reduced were associated with an increase in the occurrence of black spots (fungal infestation) on the fruit, leading to decreased fruit quality compared to the control trees.

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Hence, ants seem to play some role in reducing the amount of black spot on mango fruit. However, the underlying mechanism of this service remains unknown, although the higher fruit quality has important economic implications: mangoes without black spots are more attractive and people are prepared to pay more for them (pers. obs.). In addition, mangoes with few black spots or infections have a longer shelf life in the market (pers. obs.).

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Conclusions

The results of this study provide an understanding of how pollinator abundance and species diversity affect mango production for smallholder farms. The abundance and species richness of ants and other flower visitors were used as a measure for assessing ecosystem services which have an impact on mango yield. The study revealed that the exclusion of ants is associated with a increased in mango productivity.

At the same time, species richness of ants was negatively associated with the species richness of other flower visitors, and other flower visitors result in the highest yield. So in this case having many different ant species is in fact a bad thing for crop yield. Ant abundance and richness had decreased other flower visitor richness and amount of black spot in the ecosystem, while promoting high quality yields for subsistence farms. Our findings suggest that the two levels of land use transformation had played a role in the alteration of ecosystem services such as pollination by affecting the visitation of ant abundance on flowers.

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APPENDIX

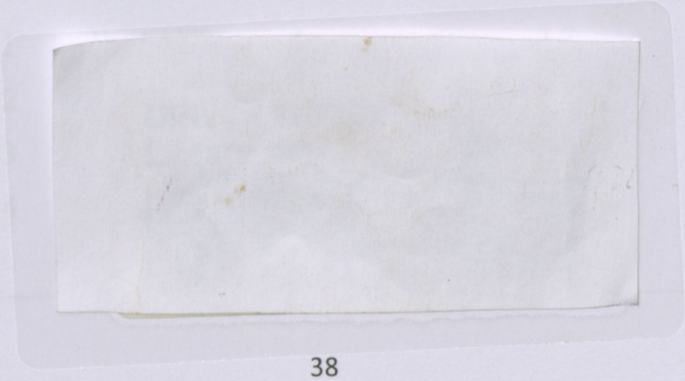
Appendix A: Orchard names, localities and land use classification.

Place	Surrouning matrix	Altitude (m above sea level)	Coordinates	
			Latitude (° S)	Longitude (° E)
Madobi	≤ 30 % natural	510	-23.18189599	30.39578296
Tshivhazwauli M	≤ 30 % natural	610	-23.08935701	30.38854502
Matieni	≤ 30 % natural	569	-23.02706497	30.43354704
Sibasa	≤ 30 % natural	678	-22.93100098	30.49789298
Tshikudini	≤ 30 % natural	568	-22.95640502	30.53105699
Vyeboom	≥ 70% natural	610	-23.14347904	30.37616001
Tswinga	≥ 70% natural	482	-23.01604302	30.46065101
Tshino	≥ 70% natural	594	-23.10637797	30.41386499
Tshivhazwauli	≥ 70% natural	628	-23.08683297	30.36644999
Tshikweta	≥ 70% natural	676	-22.93004997	30.50703001

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Appendix B: Mango yield (kg per average orchard) harvested in 9 orchards situated in two different levels (matrix ≥ 70% natural habitat and matrix ≤ 30% natural habitat) of land use transformation.

Orchard	Surrouning matrix	Date	Stand. Dev	Weight (kg) per orchard
Sibasa	≤ 30 % natural	16/11/2015	5.57	35.61
Tshikweta	≥ 70% natural	17/11/2015	8.50	14.39
Tshikudini	≤ 30 % natural	18/11/2015	4.90	5.60
Tswinga	≥ 70% natural	19/11/2015	10.57	10.13
Tshivhazwauli	≥ 70% natural	20/11/2015	18.25	18.88
Tshivhazwauli M	≤ 30 % natural	23/11/2015	17.13	28.09
Vyeboom	≥ 70% natural	24/11/2015	8.80	19.88
Madobi	≤ 30 % natural	25/11/2015	8.25	6.75
Tshino	≥ 70% natural	26/11/2015	4.33	6.31



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Appendix C: Mango yield harvested for exclusion and control trees in different size of the trees for nine orchards.

Orchard	Tree	Treatment	Tree width (m)	Tree height (m)	weight (kg)
Sibasa	1	Control	6	4.4	52.5
Sibasa	2	Exclusion	2	1.9	19.5
Sibasa	3	Exclusion	4.5	4.3	30.2
Sibasa	4	Exclusion	4.4	4.1	23
Sibasa	5	Control	6	4.2	66.1
Sibasa	6	Control	5.6	4.3	23
Sibasa	7	Control	5.7	4.1	50.5
Sibasa	8	Control	4.5	4	56
Sibasa	9	Exclusion	4.2	4	36
Sibasa	10	Exclusion	5.2	4.4	51.5
Sibasa	11	Control	5	4.2	6
Sibasa	12	Exclusion	6	4.4	13
Tshikweta	1	Exclusion	5	4.1	34.7
Tshikweta	2	Exclusion	6	4.3	12.1
Tshikweta	3	Control	4.1	5	10
Tshikweta	4	Exclusion	5	3.8	21
Tshikweta	5	Control	4.8	4.1	12
Tshikweta	6	Exclusion	5.9	4.2	5.9
Tshikweta	7	Exclusion	6	3.5	15
Tshikweta	8	Exclusion	5.8	3.9	7.9
Tshikweta	9	Control	4.5	2.5	15.4
Tshikweta	10	Control	4	3.8	16.1
Tshikweta	11	Exclusion	5	3.7	22.9
Tshikweta	12	Control	4.8	3	0.6
Tshikweta	13	Control	4	4.3	19.9
Tshikweta	14	Control	4.1	4.1	8
Tshikudini	1	Control	4.2	4.3	6

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Tshikudini	2	Exclusion	4	4.4	10.9
Tshikudini	3	Control	5	4.3	10.1
Tshikudini	4	Exclusion	3	3	7.5
Tshikudini	5	Exclusion	4.3	5	0
Tshikudini	6	Control	3.1	3.6	0
Tshikudini	7	Exclusion	4.1	4.2	5.8
Tshikudini	8	Exclusion	6	4.2	3.3
Tshikudini	9	Control	4	4.3	7
Tshikudini	10	Control	5	3.8	16.9
Tshikudini	11	Exclusion	4.5	4.2	5.5
Tshikudini	12	Exclusion	4.5	4.2	5.5
Tshikudini	13	Exclusion	3.8	3.9	0
Tshikudini	14	Control	4.2	4.4	0
Tswinga	1	Exclusion	4.4	4.3	38.5
Tswinga	2	Control	3.9	4.2	17
Tswinga	3	Exclusion	3.9	4.1	2.9
Tswinga	4	Control	3.9	3.7	3.1
Tswinga	5	Exclusion	4.3	4.4	1.9
Tswinga	6	Exclusion	4.3	4.2	13.5
Tswinga	7	Control	4	4.2	2.5
Tswinga	8	Exclusion	4.2	4	3.5
Tswinga	9	Exclusion	3.9	4.1	9.1
Tswinga	10	Control	4.2	4.3	17.5
Tswinga	11	Control	3	3.9	7.5
Tswinga	12	Control	4.3	4.2	4.5
Tshivhazwauli	1	Exclusion	5	4.3	35
Tshivhazwauli	2	Control	4.8	3.9	11.5
Tshivhazwauli	3	Control	4.9	4.1	43.8
Tshivhazwauli	4	Control	5.4	4.1	18.9
Tshivhazwauli	5	Exclusion	4.7	4.2	2.1
Tshivhazwauli	6	Control	4	4.1	32

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Tshivhazwauli	7	Exclusion	3.9	3.3	0.1
Tshivhazwauli	8	Control	3.2	3.5	49.1
Tshivhazwauli	9	Exclusion	5	4.1	29
Tshivhazwauli	10	Exclusion	4	4.1	0
Tshivhazwauli	11	Control	4.3	3.3	0
Tshivhazwauli	12	Exclusion	3.6	3.3	5
Tshivhazwauli M	1	Exclusion	4.5	3.5	13.5
Tshivhazwauli M	2	Control	4.6	3.6	16.5
Tshivhazwauli M	3	Exclusion	5	3.8	19.1
Tshivhazwauli M	4	Control	4.6	3.8	36.3
Tshivhazwauli M	5	Exclusion	5	3.8	21.1
Tshivhazwauli M	6	Exclusion	5	3.6	2.5
Tshivhazwauli M	7	Exclusion	4.5	3.7	20.4
Tshivhazwauli M	8	Control	5	3.7	39.2
Tshivhazwauli M	9	Control	5	3.7	66.5
Tshivhazwauli M	10	Exclusion	5	4	45
Tshivhazwauli M	11	Control	5	3.9	35
Tshivhazwauli M	12	Control	4.7	3.7	22
Vyeboom	1	Exclusion	4.8	3.4	21.5
Vyeboom	2	Exclusion	4	3.6	23.8
Vyeboom	3	Control	4	3.7	24.4
Vyeboom	4	Control	2.3	3.8	27.7
Vyeboom	5	Exclusion	4.1	3.8	11.1
Vyeboom	6	Control	4.7	4.3	5.9
Vyeboom	7	Exclusion	5.6	4	14.8
Vyeboom	8	Control	4.7	3.4	15
Vyeboom	9	Control	5.2	3.7	18
Vyeboom	10	Exclusion	4.4	3.5	19.5
Vyeboom	11	Exclusion	5	4.1	37.6
Vyeboom	12	Exclusion	4.2	3.7	6.5
Vyeboom	13	Control	5	3.7	24.5

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Vyeboom	14	Control	5	4	28
Madobi	1	Control	4.7	2.7	3.9
Madobi	2	Control	4.4	3.4	0.9
Madobi	3	Control	4	2.9	21.4
Madobi	4	Control	4.4	3.5	0
Madobi	5	Exclusion	3.4	4.1	19
Madobi	6	Exclusion	4.3	3.1	14
Madobi	7	Control	4.2	3.2	2
Madobi	8	Control	4.6	2.9	9
Madobi	9	Control	3.3	2.6	20
Madobi	10	Exclusion	4	2.7	0.9
Madobi	11	Exclusion	4	2.6	0.5
Madobi	12	Exclusion	4	3.2	2.5
Madobi	13	Exclusion	4.6	3.2	0.4
Madobi	14	Exclusion	5	3.3	0
Tshino	1	Exclusion	4.2	3.5	4.6
Tshino	2	Exclusion	4.2	3.5	6.9
Tshino	3	Control	4	3.6	16.8
Tshino	4	Control	4.3	33	7.1
Tshino	5	Exclusion	5	3.9	6.5
Tshino	6	Control	4	3.7	9.5
Tshino	7	Control	3.8	3.3	0.5
Tshino	8	Exclusion	4	3.6	4.5
Tshino	9	Control	3.7	3.1	0.9
Tshino	10	Control	4	2.8	1
Tshino	11	Exclusion	3.2	2.7	8.5
Tshino	12	Exclusion	3.4	3	4
Tshino	13	Exclusion	4.4	3.3	7.5
Tshino	14	Control	4.4	3.5	10

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Appendix D: Checklist of invertebrate taxa and their abundance observed on mango flowers in two different levels (matrix ≥ 70% natural habitat and matrix ≤ 30% natural habitat) of land use transformation.

Order	Family	30% natural areas	70% natural areas	Visits	Total
Hymenoptera	Pteromalidae	36	57	523	4299
	Sphecidae	16	15	116	
	Vespidae	53	32	258	
	Anthophoridae	5	7	48	
	Apidae	60	66	673	
	Braconidae	5	18	84	
	Eumenidae	4	5	24	
	Formicidae	141	50	2500	
	Ichneumonidae	1	0	1	
	Megachilidae	4	4	28	
	Pompilidae	2	0	6	
	Scoliidae	5	5	30	
	Tenthredinidae	1	1	4	
	Chrysomelidae	1	0	4	
Coleoptera	Meloidae	1	0	3	74
	Scarabaeidae	1	7	26	
	Bombyliidae	4	9	45	
Diptera	Calliphoridae	108	95	833	1663
	Muscidae	53	67	246	
	Mydidae	0	1	6	
	Sarcophagidae	9	7	40	
	Syrphidae	65	63	322	
	Tachnidae	29	34	212	
	Coreidae	4	0	4	
Hemiptera	Lygaeidae	3	0	31	32
	Tessaratomidae	0	1	1	
Lepidoptera	Nymphalidae	4	7	23	31

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	Pieridae	0	3	8	
Odonata	Gomphidae	0	2	5	8
	Libellulidae	1	1	3	
Grand Total		616	557	6107	6107

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